ECOLOGICAL SUCCESSION.

I. Stream Fishes and the Method of Physiographic Analysis.

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Contents.

I. Introduction.

The writer is interested primarily in experimental work. In connection with experiments on the modification of taxonomic characters of the tiger beetles and the life-history work which necessarily accompanied it (Shelford, '08), certain striking relations of these beetles to environmental complexes were noted in 1905. These relations corresponded closely to the environmental relations and succession of plants, and illustrated the same principles as the plants themselves (Shelford, '07). Because of possible important bearings of the facts discovered on experimental work, and the mode of attacking the problems of evolution, the writer undertook to familiarize himself with the principles of physiography, and with the principles of plant ecology as set forth by Warming, Cowles, Schimper, Clements, Whitford, Livingston, Transeau, Flahault, Schröter, Moss, Schantz, Dacknowski and many others. The work of Adams and of other zoölogists has been followed in detail also.

It was my hope to secure guiding principles to be used in the interpretation of the tiger beetle data, in the fields where zoölogy has contributed only *chaos*. In 1907 an appointment requiring that I give instruction in natural history alone, using the field method, served to stimulate my efforts in this direction in order to find a basis for the organization of field and natural history instruction. In 1908, I was compelled, quite against my will, to drop experimental work for a time and have been left free to pursue the inquiry to its logical endings.

An early training in zoölogy which was of the strictest morphological type, caused me at the outset to share the doubts of many biologists as to the value of ecological work. However, because of the circumstances just referred to, I was able to examine the work of plant ecologists with a large degree of sympathy, which has grown as the inquiry and accompanying investigations have progressed. It will be seen that we have been *investigating the question of the value and relations of organized ecology to absorbing biological problems of today*. It is the results of this investigation that we are concerned in presenting here. The zoölogical investigations which have accompanied the work have been various and only the significant results will be presented. The investigations have been carried only far enough to indicate the lines in which they may profitably be directed further.

The result of our general inquiry, while in the main gratifying, is in some respects disappointing. We had hoped to find intimate relations between organizable ecology and the absorbing biological problems of the day, but everything points to the fact that animal ecology must be organized independently first, and related to other problems after organization has been attained. For this reason and for the sake of clearness, we have separated ecology as sharply from other subjects as possible.

It should be noted at the outset that the basis, in principle, of modern ecology has been developed by botanists quite independently of other divisions of the subject of botany. Doubts as to the value of plant ecology once existed among botanists, but these have disappeared and ecology has a recognition on a level with evolution, morphology, and physiology. This is of interest here, because history often repeats itself.

In general, animal ecology is concerned with the relation of animals to their environments. The *first essential is to locate the animal in its environment.*

Our inquiry and the papers which will deal with the results have centered around the following purposes:

1. To determine the animal activity which takes place within the narrowest limits and which is most important to the species, with a view to locating motile animals in their environments.

2. To determine the phenomena in animals which correspond to growth-form in plants. Growth-form in plants is usually a convenient index of the physiological conditions within.

3. To determine the validity of ecological succession as applied to animals.

4. To determine the value of the principles of physiography and plant ecology, (*a*) in locating animals in their environments, (*b*) in determining something of the physiological character of the organism as a whole, and (*c*) in the analysis of the organism.

5. To inquire into the possibility of organizing a system of ecological classification for animals which shall be sufficiently independent of the other systems and methods, to form a basis for generalization which may serve as a check on the results of the fields of evolution, heredity, and physiology.

6. To inquire into the relation of succession to the quantitative problems of biology.

7. To inquire into the relation of succession to the origin of adaptations.

8. To inquire into the relations of ecology to the economic problems of zoölogy, and the possibility of using ecology as a means of bringing about a better unification of the various branches of zoölogy, pure and applied.

It has been found impracticable to organize the work so that one paper will deal with the subject of any one of the above propositions alone. The discussion of physiological animal geography in the Whitman Memorial Volume of the *Journal of Morphology* is intended to serve as an introduction to the general questions and deals mainly with the first two and the fifth purposes. The present paper, which is intended to be the first of a series of five or six, is concerned with the question of the

value of the principles of physiography as outlined in the fourth.

With the development of the ideas of genetic physiography came the recognition of the succession of physiographic conditions over a given locality (point *B* of Fig. 1). The relations of plants and animals to physiographic features being recognized, the first recognition of plant and animal succession came in connection with physiographic succession. Cowles ('01) carried out a complete classification of the vegetation near Chicago on the basis of the plant succession which accompanies physiographic

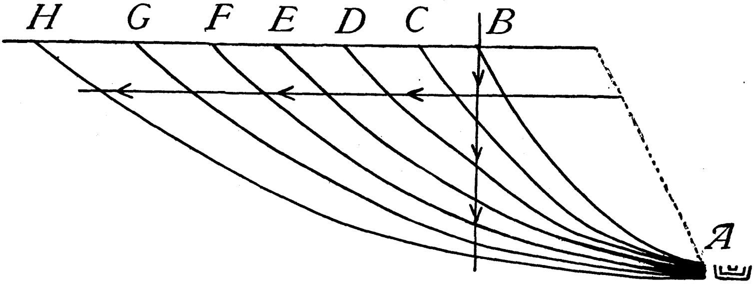


FIG. 1. A diagram showing the successive stages in the profile (general shape of the bottom) of a very young stream, curved lines, *A–B*, *A–C*, *A–D*, *A–E*, *A–F*, *A–G*, *A–H* representing the successive profiles. The uppermost horizontal line represents the surface of the land into which the stream is eroding. The horizontal line with the arrow heads indicates the direction of the migration of the source of the stream and accordingly of similar stream conditions. The vertical line with arrow heads when followed downward passess through a succession of stream conditions and represents physiographic succession at the locality *B*. The point *A* is the mouth of the stream. Opposite this are shown three successive sizes of the stream, and therefore succession at that point. The vertical scale is greatly exaggerated.

change. Adams ('01) also discussed in general geographic terms the relations of animals to base-leveling and stream development. He referred to succession of forms in streams. Since his paper, little has been done in the study of the actual relations of animals to the various stages of stream development, or the relative importance of the activities of the animals and the dynamics of streams in determining distribution.

In the study of all phases of distribution, animal activities have been usually either ignored or taken for granted. Taxonomy has been the center around which all such work has rotated and the taxonomic characters used have been very generally structural. In the study of succession this has been true, only

to a lesser degree. We believe that workers in this line have had in mind the recognition of activities, but the subject is too new to make such an ideal realizable in practice.

It is the purpose of this paper to present some details of the distribution of fish which shall throw light on the limitations and applications of the principles which Adams set forth.

The presentation of data and the discussion are based on the following questions:

1. Are the fish of the headwaters of older streams the same as the fish of younger streams?

2. If so, did they get into the stream when it was young and simply keep pace with the advance of erosion into the land?

3. What is the relation of the activities of animals to their distribution in streams?

4. What aspects of succession are of purely local and what are of general significance?

II. Localities and Material Studied.

In the investigation of problems in any field, one of the things requiring great care is the selection of material. In the study of ecology, if it is to be concerned with particular groups, this is true, and in addition a *still more important selection must be made,* namely, *that of the localities for study.*

1. *The Material.*

For this study fish were selected because they are probably the only animals that are not introduced by accidental means. They must have entered the streams studied at their mouths.

2. *The Points of Study.*

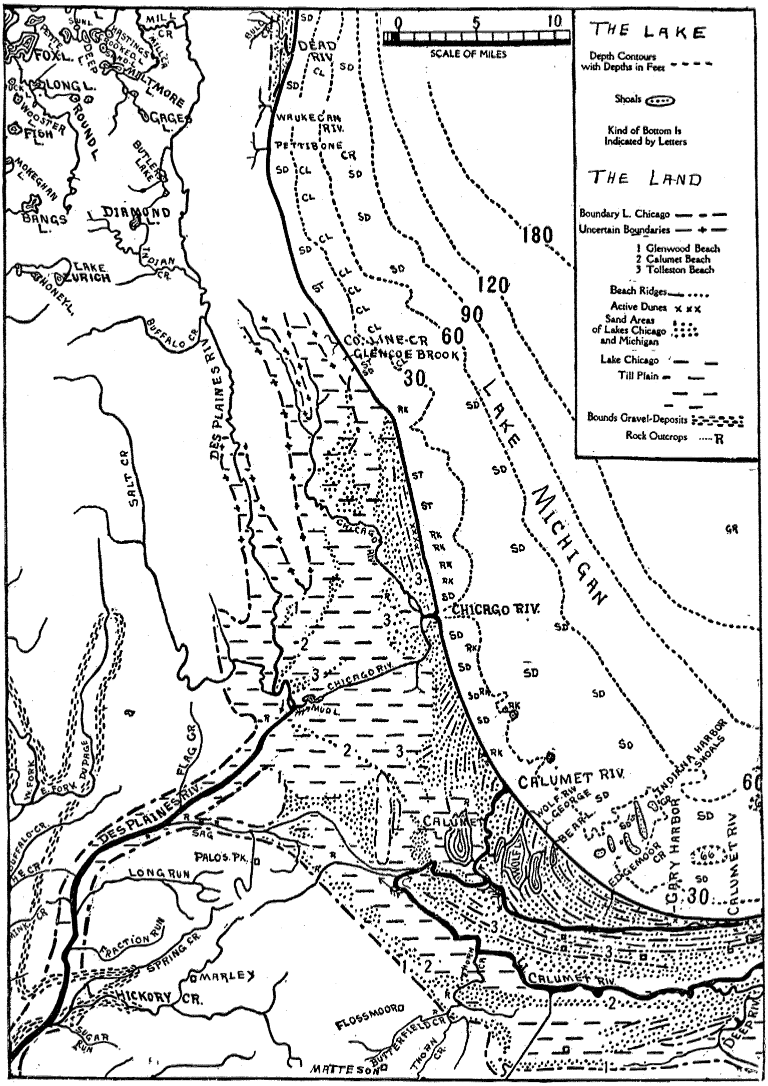
For the purposes of this study, the fish of several small streams, within forty miles of Chicago, have been collected. These streams are all indicated on the map.

(*a*) *Present Conditions.*

Beginning with the most northerly on the map, the streams are:

Bull Creek-Dead River.—It extends inward about three fourths of a mile from the boundary of old Lake Chicago (see map), and divides into two main branches, each of which has a number of

tributaries. The total distance from the old Lake Chicago bluff to the headwaters is about two and one fourth miles. Its lower



Map of the Vicinity of Chicago.

course which was added by the falling of the water of the lake, is known as Dead River.

Pettibone Creek is similar to Bull Creek, but a little smaller. Its length does not exceed one and three fourths miles.

County Line Creek is about twelve miles farther south. It differs from the others in being smaller. It also divides into two branches at a distance of only three sixteenths of a mile from its mouth and the length (with tributaries) is about one half mile.

Glencoe Brook is about one mile south of County Line Creek and has a total available length, so far as fish are concerned, of only a few rods.

These four streams are closely comparable. They all rise in a moraine which stands between 60 and 100 feet above the lake. Its height at the lake, or point nearest the lake, is about 60 feet in every case. With the exception of the lower courses of Bull Creek and Pettibone Creek, all are composed of strictly intermittent riffles and permanent (except in unusual seasons) pools. We will refer to these as the North Shore streams. In addition to these, two other streams were studied for comparison—Thorn-Butterfield Creek and Hickory Creek, including its west branch.

Hickory Creek is very different from the others. It drains a number of marshes and is permanent. Its upper course is larger than that of the north shore streams; it is sluggish and meanders through prairie marshes with only a very slight fall. The level of this part of the stream represents that of a depression between glacial ridges (Goldthwait, '09). So far as the present cycle of erosion is concerned (Salisbury, '07), erosion has proceeded as far as Marley. Below this point the stream is a typical swift brook.

Thorn-Butterfield Creek is intermediate between Hickory Creek and the north shore streams. The southern branch of Butterfield Creek, near Matteson, Ill., is sluggish, but has intermittent riffles and permanent pools.

(*b*) *History of the Region.*

When the Wisconsin ice sheet retreated from its maximum extent, which lay beyond the center of the state of Illinois, the edge of one of its lobes (Atwood and Goldthwait, '08) took up a position a few miles outside of, and parallel with, the present

shore of Lake Michigan. Here it deposited what is known as the Valparaiso Moraine. When the ice retreated from this position, it occupied the basin of Lake Michigan a little to the north of the present south end of the Lake. Water occupied the space between this lobe and the Valparaiso Moraine. This body of water is known among geographers and geologists as Lake Chicago. At its period of maximum extent (see map), it stood 55 to 60 feet above the present lake. The history of Lake Chicago and the other predecessors of Lake Michigan is complicated

TABLE I.

SHOWING THE DISTRIBUTION OF FISH IN THE NORTH SHORE STREAMS AT THE TIMES INDICATED. The numbers refer to Fig. 2 and Fig. 4.

Name of Stream and Common Name of Fish.	Date and Scientific Name.	1	2	3	4	5	6	7
Glencoe Brook	August, 1907							
Horned dace	*Semotilus atromaculatus*	*						
County Line Creek	1907–8.							
Horned dace	*Semotilus atromaculatus*	*	*	*	*			
Blacknosed dace	*Rinichthys atronasus*			*	*			
Johnny darter	*Boleosoma nigrum*			*	*			
Blackhead minnow	*Pimephales promelas*				*			
Bluntnosed minnow	*Pimephales notatus*				*			
Common sucker	*Catostomus commersonii*				*			
Pettibone Creek[1]	September, 1909, and April, 1910.							
Horned dace	*Semotilus atromaculatus*	?	*	*	*			
Red bellied dace	*Chrosomus erithrogaster*		*	*	*			
Blacknosed dace	*Rinichthys atronasus*			*	*			
Johnny darter	*Boleosoma nigrum*			*	*			
Common sucker	*Catostomus commersonii*				*			
Bull Creek-Dead River	September, 1909.							
Horned dace	*Semotilus atromaculatus*	*	*	*	*	*		
Red bellied dace	*Chrosomus erithrogaster*		*	*	*			
Blacknosed dace	*Rinichthys atronasus*			*	*			
Common sucker	*Catostomus commersonii*				*	*		
Bluntnosed minnow	*Pimephales notatus*					*	*	
Little pickerel	*Esox vermiculatus*					*	*	*
Blue gill	*Lepomis pallidus*						*	*
Large mouthed black bass	*Micropterus salmoides*						*	*
Pike	*Esox lucius*							*
Crappie	*Pomoxis annularis*							*
Red horse	*Moxostoma aureolum*							*
Chub sucker	*Erimyzon sucetta*							*
Golden shiner	*Abramis crysoleucas*							*
Common shiner	*Notropis cornutus*							*
Cayuga minnow	*Notropis cayuga*							*
Tadpole cat	*Schilbeodes gyrinus*							*

[1] The lower part of Pettibone Creek has been destroyed by the U. S. Naval School otherwise the table would include the records for a point 5 and perhaps a point 6, but probably not 7. ? indicates incomplete identification.

and it will suffice, for our purposes, to state that the level of the water fell to a point about 40 feet above the present Lake Michigan. After standing in this position for a time, it fell again to a point 20 feet lower. Its next period of standstill was at a 12-foot level from which it receded to the present lake level.

The oldest of the north shore streams probably began as mere gullies when the lake was at its 60-foot level. These gullies have worked their way back into the morain and deepened their channels in the manner described by Adams ('01) and diagrammatically illustrated in Fig. 1. Long ago Bull Creek was similar to the present County Line Creek. At a recent period County Line Creek was also like Glencoe Brook.

There have been some modifications of these processes caused by changes in lake level. Each time the level of the lake fell, the streams were left with a steep portion near the mouths. Under

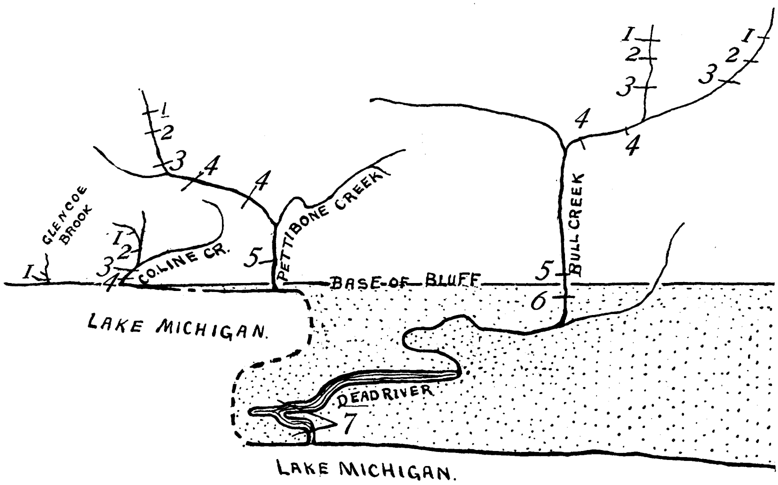


FIG. 2. Diagrammatic arrangement of the north shore streams. The streams are mapped to a scale of one mile to the inch and the maps are placed as closely together as possible in the diagram. The intermediate shore-lines are shown in broken lines which bear no relation to the shore lines which exist in nature. Toward the top of the diagram is west.

Each number on the diagram refers to the pool nearest the source of the stream which contains fish, as follows; 1, the horned dace (*Semotilus atromaculatus*); 2, the red-bellied dace (*Chrosomus erythrogaster*); 3, the black-nosed dace (*Rinichthys atronasus*); 4, the suckers and minnows; 5, the pickerel and blunt-nosed minnow; 6, the sunfish and bass; 7, the pike, chub, sucker, etc. The bluff referred to is about 60 feet high. The stippled area is a plain just above the level of the lake.

such conditions the steep portions migrate back into the moraine, *i. e.*, up stream, until the source is reached. The process of lowering the water level at the mouth of a stream and the development of the steep portion is known as rejuvenation. Rejuvenation usually affects the distribution of fishes in streams.

However, streams which are made up of intermittent pools and riffles are not so much affected as larger streams. Furthermore, softness of the glacial clay in which the north shore streams are located would cause the changes in the stream bed to take

Table II.

The Distribution of Fish in Hickory Creek (and its West Branch) in the Summer of 1909.

Those starred were in the pool nearest the source. I., The first mile of the stream, measured from the fish pool nearest the source, toward the mouth; II., the third and fourth miles; III., at the head of erosion, five miles from the pool nearest the source; IV., six miles from the pool nearest the source; V, nine miles from same; stream much larger with good riffles and one weedy cove.

		I.	II.	III.	IV.	V.
Horned dace*	*Semotilis atromaculatus*	*	*	*	*	*
Golden shiner*	*Abramis crysoleucas*	*	*		*	
Johnny darter*	*Boleosoma nigrum*	*	*	*	*	
Stone roller*	*Campostoma anomalum*	*	*	*		*
Straw colored minnow*	*Notropis blennius*	*	*		*	*
Blue spotted sunfish*	*Lepomis cyanellus*	*	*	*		*
Blunt nosed minnow	*Pimephales notatus*	*	*	*	*	*
Common sucker*	*Catostomus commersonii*	*	*			*
Mud minnow	*Umbra limi*		*			
Top minnow	*Fundulus notatus*		*	*		
Red bellied dace	*Chrosomus erythrogaster*		*	*		
Chub sucker	*Erimyzon sucetta*		*		*	
Black bullhead	*Ameiurus melas*		*			*
Black fin	*Notropis umbratilis*			*	*	
River chub	*Hybopsis kentuckiensis*			*	*	*
Fan tailed darter	*Etheostoma flabellare*			*	*	*
Rainbow darter	*Etheostoma cœruleum*	*		*	*	*
Least darter	*Microperca punctulata*				*	
Sucker mouthed minnow	*Phenacobius mirabilis*				*	
Cayuga minnow	*Notropis cayuga*				*	*
Rock bass	*Ambloplites rupestris*				*	*
Common shiner	*Notropis cornutus*					*
Rosy faced minnow	*Notropis rubifrons*					*
Banded darter	*Etheostoma zonale*					*
Blue gill	*Lepomis pallidus*					*
Long eared sunfish	*Lepomis megalotis*					*
Stone cat	*Noturus flavus*					*
Yellow perch	*Perca flavescens*					*
Small mouthed black bass	*Micropterus dolomieu*					*
Hogsucker	*Catostomus nigricans*					*
Common red horse	*Moxostoma aureolum*					*

place rapidly. In the existing streams the slope of bed differs within a given stream and with respect to the different streams. The differences do not appear to be of importance in determining the relations of the fish present to a stream as a whole. Accordingly, we shall not consider the effect of rejuvenation in the discussions following.

III. Presentation of the Data.[1]

Data of the kind upon which this paper is based are doubtless familiar to all collectors of fish. From our point of view the presence or absence of a given species is not of particular importance, but we are concerned with the *arrangement* of fish in the streams and its causes. Such causes cannot be discussed here because they should be studied experimentally. As yet we have not been able to do this.

Fig. 2 shows the streams and Table I. the distribution of the fish in these streams.

1. *Discussion of Table I.*

We note that the fish (horned dace) of the smallest stream (Glencoe Brook) belong to the same species as those at the head-

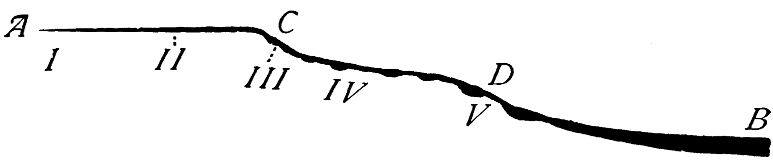


FIG. 3. Diagrammatic profile of Hickory Creek. *A*, source; *B*, mouth; *C*, head of erosion; *D*, rock outcrop. The figures below refer to the columns in Table II. and represent parts from which fish were collected.

waters of the larger streams. The red-bellied dace, when present, is not found so far upstream as the horned dace. The red-bellied dace is absent from County Line Creek. Since all the fish in all the streams must have entered from Lake Michigan, one is

[1] The fish of County Line Creek were collected and their arrangement studied from time to time between 1907 and 1910. The arrangement of the fish as shown by the map of the stream was about the same throughout the periods of study, and Table I., except for the drought of 1908. The collections from the other streams were made in the summer and autumn of 1909, partly with the assistance of Mr. S. F. Hildebrand, of the Field Museum of Natural History.

surprised that they have found so many of the streams as is indicated here. The absence of the red-bellied dace is no doubt due to accident.

The black-nosed dace is present in all the streams except Glencoe Brook, but lower down than the two just mentioned. It is usually accompanied by the Johnny darter, which is absent from Bull Creek. This absence is probably due to the same causes as the absence of the red-bellied dace from County Line Creek. The Johnny darter probably had never become established in County Line Creek; only two specimens have been taken and opportunities to secure a complete collection were good when the pools dried.

Records of the occurrence of the blunt-nosed and blackhead minnows in County Line Creek are based on a single specimen of each taken by a student from the pool nearest the mouth of the stream. We have taken no others and these were probably not residents.[1] We note that at the points marked 4 (Fig. 4) as shown in column 4, all the fishes occurring nearer the source of the stream are present and in addition the young of the common sucker.

In Bull Creek at point 5, as shown in column 5, the daces are represented by the horned dace alone; the other two being absent. The minnows were present here in numbers and evidently regular residents. The little pickerel was not abundant.

In columns 6 and 7 (see map also), we find the record of a number of fishes belonging to large creeks and to ponds. The distribution of the fishes in Table I. corresponds to the habitat preferences indicated by Forbes and Richardson ('08), pages cix to cxiii.

2. *Discussion of Table II.*

By comparing columns 1 to 6 in Table I. with column I. of Table II., we note that nearly all the fish present in the north shore streams are present at the point nearest the source of Hickory Creek. Considering the first, third and fourth miles of this stream we note that, the little pickerel and the black-nosed dace are absent in the preërosion part of Hickory Creek

[1] Hankinson has pointed out the difficulties of securing a complete collection of fish. He sees fish in the water which he has difficulty in securing with a dip net.

and present in the north shore streams. In addition, we find several species in Hickory Creek (among these is a single specimen of darter, the species probably not resident) not found in the north shore streams at all. Hickory Creek is better situated for fish to enter, as they may come upstream directly, while in the north shore streams they must enter the lake and enter a given stream by chance. Accordingly, the larger number of species is to be expected in Hickory Creek.

In column III. are shown the fishes at the head of erosion or the riffles nearest the source of the stream. A number of swift-water fish—darters—are shown here. These were abundant.

In column IV. the occurrence of a number of fishes similar in habits to those shown in column III. is indicated. The stream is similar in bottom and volume of water at the localities represented in columns III. and IV., and further collecting would probably have shown these two localities to be inhabited by practically the same fish. The rock bass was represented by a single juvenile specimen.

Column V. shows the fish at a point in the stream where the volume of water is about four times that at point IV. The stream here is characterized by riffles and large pools. This was more thoroughly studied. Collections were made several times during the season and daily for nearly a week in the month of September, 1908. Here was taken a single juvenile specimen of the horned dace. The red-bellied dace and Johnny darter were not taken. The addition of a number of larger fishes here is of interest. These additional species are characteristic of large streams.

3. *Discussion of Table III.*

Table III. is introduced to show conditions intermediate between the north shore streams and Hickory Creek. The localities of study were selected to correspond to localities in Hickory Creek, just so far as conditions in Thorn-Butterfield Creek would permit. In general, conditions at A in this stream correspond to I. in Hickory Creek, but differ in that the water at A is confined to pools in dry weather and is continuous at I. B corresponds to III. and C to V.

An inspection of column A shows that some of the same fishes are present as in the uppermost pool of Hickory Creek. Again there are certain differences. These differences are the absence of certain fish—the Johnny darter, the golden shiner, the straw-colored minnow and the common sucker. The presence of these at locality I. of Hickory Creek is probably due to the artificial exposure of bare bottom.

Table III.

The Fish of Thorn Creek Collection Made at the Headquarters in 1908 and 1909 and at Other Points in 1909 and 1910.

A, The first fish pool; B, four miles down stream; C, ten miles down stream.

		A	B	C
Horned dace	*Semotilus atromaculatus*	*	*	*
Blunt nosed minnow	*Pimephales notatus*	*	*	*
Blue spotted sun-fish	*Lepomis cyanellus*	*	*	*
Stone roller	*Campostoma anomalum*	*	*	*
	Notropis umbratilis		*	?
Banded darter	*Eheostoma zonale*		*	?
Common shiner	*Notropis cornutus*		*	?
Striped top minnow	*Fundulus dispar*		*	?
Black sided darter	*Hadropterus aspro*		*	*
Johnny darter	*Boleosoma nigrum*		*	*
Mud minnow	*Umbra limi*		*	*
Cayuga minnow	*Notropis cayuga*		*	*
Golden shiner	*Abramis crysoleucas*		*	*
Large mouthed black bass	*Micropterus salmoides*			*
Small mouthed black bass	*Micropterus dolomieu*			*
Blue gill	*Lepomis pallidus*			*
Crappie	*Pomoxis sparoides*			*
Pirate perch	*Aphredoderus sayanus*			*
Yellow perch	*Perca flavescens*			*
Carp	*Cyprinus carpio*			*
Black bull head	*Ameiurus melas*			*
Common sucker	*Catostomus commersonii*			*
Short-headed red horse	*Moxostoma breviceps*			*
Pike	*Esox lucius*			*

Comparison of this list with that of the north shore streams (except 6 and 7) shows that, in so far as the north shore species are in Thorn-Butterfield at all, they are at the headwaters with the exception of the Johnny darter.

In column B we note that the fish are about the same species as were found in localities III. and IV. in Hickory Creek, in so far as they have been found in both streams at all. *Notropis cornutus* is found further upstream in Thorn-Butterfield Creek than in Hickory Creek.

In column C we note a number of fishes, twenty species and four doubtful identifications, as against twenty-two at point V. in Hickory Creek. Ten of these are the same in the two streams. Again we find larger fishes in the large parts of the stream.

IV. Discussion of the Data.

It is easy to lose oneself in the maze of taxonomic diversity which one finds in a number of streams separated no further than the ones considered here. We are not concerned with taxonomy. The suggestions and inferences herein are chiefly to illustrate a method of analysis and to suggest a method of combined experimental and field study. It should be borne in mind throughout the discussion that ecology as an organized science is in much the same state as morphology was when it was necessary to discuss methods which are now taken for granted.

1. *Distribution of Fishes in the Streams.*

We will consider the north shore streams first. We have noted that they are similar to each other in origin, in materials eroded, in their relations to the lake, and in being for the most part made up of permanent pools and intermittent riffles. An inspection of Table I. shows that there is a definite arrangement of fishes in these streams. Furthermore, that there is a close correspondence between the upper courses of the different streams in the matter of the fishes present, as well as in their arrangement. The *only* species, the horned dace, in the youngest stream (Glencoe Brook) is the same as the species which is *nearest the source of all the other streams.*

There are some differences in the fish communities of corresponding parts of the different streams, but these are probably due to the failure of a given species to enter a given stream. One is struck with the similarity of the corresponding fish communities rather than the differences.

In making a general comparison, reference to the diagram of the maps of the streams (Fig. 2) shows that the different *fish communities* are *closer* together in the smaller streams. Fig. 1 shows that the slope of the bed of the young streams is greater

than that of the older streams, and the different *conditions* accordingly closer together.

Turning to the other two streams studied (Hickory Creek and Thorn-Buttterfield Creek), we see that the same species, the horned dace, is at the headwaters of these, as at the headwater of the north shore streams. It is accompanied, however, by several other species, a part of which are found in the north shore streams at points further down stream and in a larger volume of water than some individuals of the horned dace. In other words the species of the north shore streams are crowded together in streams where the volume of water is greater at the headwaters than in the north shore streams.

(*a*) *Causes of the Definite Arrangement of the Fishes in the Streams.*

The arrangement of the fish in these streams suggests definite reactions to some factor or factors in the stream. Rheotaxis is suggested as a cause of the upstream movement, and water pressure and size of stream a factor limiting the upward movement. This should be studied experimentally.

(*b*) *Origin of the Fish Communities.—Migration.*

A discussion of the mode of origin of the fish communities is concerned with the mode of entrance of the fish into the habitat. While manner of entrance of fish into a stream is not of particular importance to us, it follows from a reference to Fig. 1 that fish may enter when the stream is young and keep pace with erosion. Fish entering when a stream was at the youngest stage indicated in Fig. 1, need only maintain their position against the current and they would be carried inland as the source of the stream migrated inland. In the case of Bull Creek, the horned dace is absent from the lower portion (Dead River) so far as our collections show. Did this species enter when Bull Creek was similar to Glencoe Brook? This is improbable for the condition in Bull Creek, when it was similar in size to Glencoe Brook, must have been similar to conditions now found near glaciers, *e. g.*, Greenland.

There is further evidence as to the improbability of such early entrance in the data of Hickory Creek fishes. We have noted that

Hickory Creek rises in a depression between two morainic ridges, and that its upper course is sluggish and did not originate by stream erosion. Its profile is shown in Fig. 3, page 19.

The species of fish now at the source of this stream could not have entered when this stream was young and have kept pace with the migration of conditions, because if this was a stream at all during the close of the glacial epoch, it was carrying the waters from melting ice or a pond in the same manner as it is now draining a marsh.

The fishes or species of fish that are now found near the source of this stream were obliged to travel a distance of five miles through a mucky marshy stream to reach the headwaters. The success of most of the species present in the sluggish upper course of this stream is probably due also to local artificial exposure of gravel, since the settlement of the country. There has been dredging to facilitate drainage. Six of the thirteen species are known to use bare bottom for breeding. Forbes and Richardson show that of the ten of these which they considered in their tables (pp. cix–cxiii) nine show a preference for the bottom of rock and sand. Some of these preferences are very decided.

This shows that fish may enter the headwaters of streams without particular reference to physiographic conditions. Here positive rheotaxis may be a factor again (Lyon, '04).

The observations of the effect of drought and flood throw further light on the cause and rate of migration.

(*c*) *The Effect of Drought and Flood on the Arrangement of Fishes in Streams.*

1. *Droughts.*—There was an unusual drought in the autumn of 1908. The data on the distribution of fishes in Glencoe Brook and County Line Creek were collected before this date. Table IV. shows the arrangement *after* the drought.

County Line Creek was entirely dry except the pool nearest its mouth in September, 1908. This is the locality marked 4 in Fig. 2. The following spring was one of normal rainfall. *The fish proceeded upstream a distance of only three rods.* This partially restored the usual arrangement. If this represents the rate, fish proceed upstream slowly. Glencoe Brook has not recovered its fish.

TABLE IV.

LOCALITIES ON THE BASIS OF THE DISTRIBUTION OF FISH BEFORE THE DROUGHT. (SEE TABLE I.)

Name of Stream and Common Name of Fish.	Date and Scientific Name.	1	2	3	4
Glencoe Brook—no fish......	October, 1909.				
County Line Creek.	September, 1909.				
Horned dace...............	*Semotilus atromaculatus*.......			*	*
Black nosed dace..........	*Rinichthys atronasus*..........				*
Common sucker...........	*Catostomus commersonii*.......				*

2. *Floods.*—Abbott ('70) collected the fishes from source to mouth of a small stream. After a flood he found none of the same fish but species belonging to larger streams. Unfortunately, he does not state that he again studied the stream from source to mouth, and accordingly leaves the question of a general upstream migration unsettled.[1]

2. *Succession.*

Ecologists are frequently asked what is meant by succession and what is the significance of succession. In answering the first part of the question there has often been a confusion resulting from a lack of distinction between the different uses of the term succession. It is used in three distinct senses. We speak of (1) *ecological succession*, (2) *seasonal succession*, and (3) *geological succession* (Adams, '09).

1. Geological succession is primarily succession of species throughout a period or periods of geological time. It is due

[1] As evidence of upstream migration of mollusca, the following seems to be important. Frequent examination of a section of the North Branch of the Chicago River at Edgebrook, between 1903 and 1907, showed that *Pleurocera elevatum* and *Campeloma* occur in this stream. *Pleurocera* was not found during this period (ending November, 1907) above a certain point. *Campeloma* was found only sparingly above this point. The spring of 1908 was one of heavy rainfall and the streams were in flood from April to June. On July 6 the snail *Pleurocera* was found in numbers one fourth of a mile further upstream, than formerly. *Campeloma* had gone nearly as far. The season from November to April was not different from other seasons and there is no reason to assume that the migration began before the spring floods. If this is true the snails could make their way toward the headwaters at the rate of at least a mile per year, if they were introduced into a large stream. This must be a response to both water pressure and current. The small value of such single observations is recognized, but they are presented here because the opportunity to secure such data is small.

mainly to *the dying out of one set of species and the evolution of others which take their places.*

2. Seasonal succession is the succession of species or stages in the life-histories of species, over a given locality, due to *hereditary and environic differences in the life-histories* (time of appearance) of the species living there.

3. Ecological succession is the succession of ecological types (physiological types, modes of life) over a given point or locality, due to changes of environmental conditions at that point. From this point of view *we have nothing to do with species except that names* are necessary. There are of course relations between these three phenomena but these relations are of the nature of checks in method of study rather than essentials, and space will not permit us to discuss them here. There are also qualifications of a similar nature that might be made to the definitions. With reference to the statement that species are irrelevant to the question, a word should be added. If the habits of a species are a part of the definition of that species, as they must sooner or later come to be, then species are significant. The definition applies to the manner in which the species question is treated in practice.

We have noted the migration aspect of the relation of fish in small streams. Succession is but a different point of view. Succession of fish means succession of established forms, *i. e.*, of forms that make the stream their regular abode. The most important aspect of establishment is breeding. A number of writers have discussed the breeding habits of the species found in these small streams (Eigenmann, '95; Forbes and Richardson, '08; Hankinson, '07, '10; Reighard, '08; Reeves, '07; Smith, '08).

(*a*) *Statement of Ecological Succession.*

Succession in the case before us is a reconstruction. It is based on the superposition of all the fish communities over the oldest part of the oldest and largest stream. To make this clearer, we will state with the aid of the diagram (Fig. 4) the succession of fish in Bull Creek. This succession will be considered as taking place over the oldest part of the portion of Bull Creek which lies back of the bluff of the former and higher levels of Lake Michigan. This is the point designated as 5.

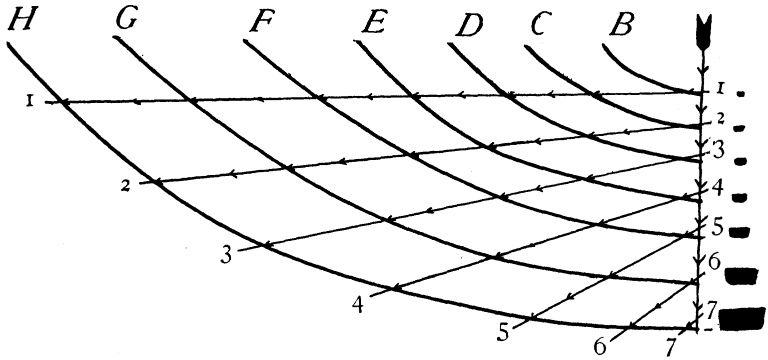


FIG. 4. This figure is based on Fig. 1. The profiles of the streams shown there are here separated vertically at the mouth. The curved lines represent seven stream stages as follows: *B*, Glencoe Brook; *C*, hypothetical stage; *D*, hypothetical stage; *E*, County Line Creek; *F*, Pettibone Creek; *G*, hypothetical stage; *H*, Bull Creek-Dead River. The hypothetical stages could, no doubt, be found along the shore of Lake Michigan, the difficulty arises from the introduction of sewage into so many streams.

The comparative size of the mouth of each stream stage is represented by a stream cross-section at the right.

The direction of reading in succession is indicated by the vertical line with the arrow heads pointing downward. The oblique lines marked 1–1, 2–2, 3–3, etc., pass through points in the stream profiles which are in the same physiographic condition, and which are occupied by similar fish communities.

When Bull Creek was at a stage represented by the first stage in our diagram (which is now represented by the present Glencoe Brook) its fish, if any were present, were ecologically similar to those now in Glencoe Brook in their relations to all factors except climate. This ecological type is represented by the horned dace alone. As Bull Creek eroded its bed and became hypothetical stage C of the diagram, the fish community of stage B was succeeded by a fish community *ecologically similar* to the fish communities at the localities marked 2 in Figs. 2 and 4. The fish now ecologically representing this community are the horned dace and the red-bellied dace. The community of the single species, the horned dace, had at such a period moved inland to the point where line 1–1 crosses the curved line representing the profile of hypothetical stage C.

As erosion continued the fish community ecologically represented by the horned dace and red-bellied dace moved gradually inland and was succeeded by a fish community occupying the

mouth of hypothetical stage D, ecologically similar to that now found at the points 3. This is represented by the three daces and the Johnny darter.

As the hypothetical stage D eroded its bed and became stage E, which is represented by County Line Creek, fish community 3 was succeeded by a fish community ecologically similar to the fish community now present at points 4. This is ecologically represented by the three daces, the Johnny darter and the young of the common sucker. The fish communities designated as 1, 2, and 3 had meanwhile moved inland and were arranged in the order which their ecological constitution required.

The continuation of the process resulted in displacing a fish community ecologically similar to the fish community 4 by a fish community ecologically similar to the present fish community 5. This is represented in the lower waters of Bull Creek by the blunt-nosed minnow and the little pickerel. Before the destruction of its lower course, Pettibone Creek should have contained this community and represented stage F.

Ecological succession is one of the few biological fields in which prediction is possible. We may carry this discussion a little further. We have noted that the developing streams continue to erode their beds, grow larger, and bring down the surface of the land. These processes have not stopped in Bull Creek; it will become larger, contain a larger volume of water at the locality 5, and the fish community of locality 5 will be succeeded by a fish community ecologically similar to that now at locality 6. It is ecologically represented by the sunfish and bass present. This stage has been designated as hypothetical stage G in the diagram. With a further continuation of the process, the fish community of stage G, locality 6, will be succeeded by a fish community ecologically similar to that now found at the locality 7 (Bull Creek-Dead River. Stage H). The fish are shown in column 7, Table I.

(*b*) *Method and Principle.*

The discussion above is intended to illustrate a method of analysis as well as to illustrate the principles involved. In order to make both clear, more fish communities have been noted than

otherwise would have been justified. It is important to recognize how much of the reconstruction is method, and how much is biological principle.

1. *The Biological Principle.*—The biological principle involved is one well recognized, but lacking in detailed and definite experimental confirmation. It may be stated as follows: Ecologically comparable animals living under similar conditions possess certain similarities of physiology, behavior, habits and mode of life.

Indirect evidence for this seems adequate for the purposes of this paper, but we have as yet been unable to conduct experimental studies in this line. The process of securing data to illustrate the principles involved here has not been small.

An obvious difficulty arises in securing language suitable for a brief expression of all that is included in physiology, behavior, habits and mode of life. The term *form* covers all matters of structure, size, proportion and in common usage, color also. As opposed to this and as covering all the physiological, and behavior characters just referred to, we will use the Latin word *mores*.[1] The *mores* of a *species* or *community of species* are not independent of the *form* or *forms:* the two are correlated, for every *mores*, we may expect to find some kind of structure, and for every form of structures, we must also expect to find some physiological differences. Our present methods may not detect these correlations between *form* and *mores* and the correlations may not be important, but the existence of such correlations seems to be a necessary assumption.

In such a series of streams as the north shore streams, it is a well-known fact that the conditions in the young streams are like those (near the headwaters) of the larger and older ones. It was for this reason that this series of streams was selected for the study. Since the same species of fish are present in like conditions, we have evidence for the uniformity of physiological make up. Since different species occupy different positions in the nicely graded series of complexes, we have an index of their comparative physiological make up which could not be easily detected by other means. We have located the animals in their

[1] *Mores:* behavior, customs. The word will be used as a collective noun exactly as form and forms are used in biology.

environment, the first essential in study of their environmental relations.

2. *Method.*—The method of analysis employed in this paper is based on physiography. The relation of physiography to ecology in this case is analogous to the relations of the microtome to anatomy, the electric needle to experimental morphology, and reagents to physiology. Ecology is in much the same state as was morphology when extensive papers and treatises on methods were necessary.

The object of this type of analysis and of locating the animal in its environment, is to determine the *physiological character of the animal as a whole.* The method of procedure is through the study of the complex conditions in which the organism is most nearly in physiological equilibrium. Some progress in the actual analysis of the organism can doubtless also be made by this method. Variation and modification of physiological make up may also be detected. Physiographic analysis is then a biological method. However, both the organism and the environment must be analyzed much further. In this further analysis the succession or the evolution of the environment is an important background and must form the basis for the selection of points of study, for comparison of results and organization in general.

Among geologists and some biologists, the presence of the same or similar taxonomic groups is often taken to indicate similarity of conditions. While ecologists must sometimes follow this method of reasoning, their method of procedure is in the main reversed. The *conditions* are studied and the presence or absence of a given set of organisms noted. In such a detailed set of conditions as these with which we are dealing, the old line of reasoning should not be followed. The modifiability of behavior speaks against it.[1] This is not a contribution to physiography. The physiography involved is well known to elementary students of that subject.

Physiographic analysis is a method like all other methods of science—to be improved, modified or rejected, according as it has

[1] *Asellus communis*, the common isopod, occurs in both ponds and streams. Mr. W. C. Allee has found that the behavior characters of the individuals inhabiting the streams and ponds are different. He has partially changed the stream *mores* to pond *mores* by keeping them in pond conditions and vice versa.

served its purpose or shows its defects. It is not, however, the only method of ecology, and it should not be employed alone, but accompanied by experimentation.

This same method may be employed in the study of the historical problems of biology, or to the study of evolution, but the results are not ecology because this method is employed. Nor is there any intimate dependence between the fundamental things in ecology so far as its progress as a science is concerned, and the divisions of biology known as evolution, morphology, or faunistic geography.

Physiographic analysis is only a part of a more general method of deducing succession and laying a foundation for comparisons. The general method of successional study has a probable significance which lies beyond the recognition of the physiological characters of organisms as a whole and the analysis of organisms as far as the method will permit.

(*c*) *The Significance of Succession.*

It will be noted that in the above statement of succession no reference to species is made. Species in the morphological sense can have only the most local significance in succession. Species inhabiting similar stages in the physiographic succession of streams, *i. e.*, similar conditions—will hardly be the same within a very small area. It appears that the idea of succession has been regarded as having little significance for this reason. A point of significance is the character of the *mores*. In the matter of their *mores* the fish communities of a stream in Europe, a stream in Japan, and a stream in the United States are probably similar if the streams are similar—a matter for experimental verification.

A science with only one method of classifying its data must constantly fall into error. Up to the present we have but one organized general system of classification for zoölogical materials, namely taxonomy. Taxonomy has been over-emphasized and carried into fields where it does not properly belong. It has given us, among other things, what has been called *composite natural history*. Composite natural history constitutes a large part of the natural history of today, especially as contained in general works on natural history. The development of a composite

natural history generalization consists in discovering that certain habits are characteristic of a few known (as to habits) members of a given taxonomic group of animals, in striking a sort of general average of the known habits of the members in question and putting such an average into the form of a general statement to apply to all the group, known or unknown. Such generalizations have their place in didactics, but they are the most inaccurate phase of zoölogy. Though often used as a basis for generalization, generalizations based upon them have a questionable value.

The crucial question before us is, then, Can we, on the basis of ecological succession or other natural basis, classify and compare animal *mores* and make generalizations on the basis of such classification and comparison? If investigation answers in the affirmative, we may organize a general system for the classification of zoölogical materials which shall be sufficiently independent of other methods and systems of classification to serve as a means of throwing additional light on the generalizations of other zoölogical fields, such as physiology, heredity, or evolution. Indeed, plant ecologists have progressed far with such a classification (Warming, '95; Cowles, '01, and many others). Their results are now recognized as of much importance by botanists generally. The logic and method back of their classification is the same as ours. The differences lie in the fact that differences in physiological make up in plants is usually indicated by vegetative *form* while differences in physiological make up in animals is indicated by differences in *mores*.

Ecological succession has not as yet been studied experimentally. Experimental studies, if properly conducted, will answer the question of the significance of all the propositions here presented. Such experimentation should be conducted with reference to an *analyzed environment* and should consist of the comparison of the *mores* of animals of different and of similar environments.

V. Summary.

1. Fishes have definite habitat preferences which cause them to be definitely arranged in streams which have a graded series of conditions from mouth to source.

2. Beginning at the sources of the streams of the developmental series considered, we find the same species represented in essentially the same order in all the streams, in so far as the series of conditions is present. The only species in the youngest stream is the same as the species nearest the sources of the larger streams.

3. Migration of conditions for breeding is an important cause of fish migration, but fish reactions outside the breeding season may be often more important than movement of conditions necessary for breeding over the route of migration. Migration may even be due to reactions to a single factor.

4. Fish entering a stream will take a position in the stream suited to their ecological constitution without regard to the time and mode of origin of these conditions.

5. There is a succession of ecological types over a given point. Ecological succession is based on similar *mores* (physiology, behavior, habits and mode of life) of fish communities as a whole or comparable species of communities.

6. Physiographic analysis locates the animal in its environment and is but a method of studying the organism as a whole and a basis for proceeding to its analysis.[1]

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